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## **Movement ecology of aerial insectivorous birds**

### **Individual-based studies on swifts and nightjars**

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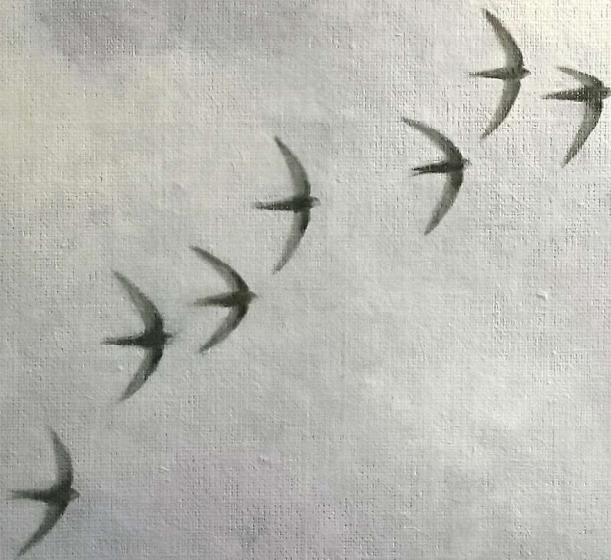
# Movement ecology of aerial insectivorous birds

Individual-based studies on swifts and nightjars

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GABRIEL NOREVIK

FACULTY OF SCIENCE | DEPARTMENT OF BIOLOGY | LUND UNIVERSITY



## Movement ecology of aerial insectivorous birds



# Movement ecology of aerial insectivorous birds

Individual-based studies on swifts and nightjars

Gabriel Norevik



**LUND**  
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DOCTORAL DISSERTATION

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<p>Abstract: Many birds are predisposed to annually undertake movements over large temporal and spatial scales. They have an efficient flight machinery, demonstrate impressive capacities in storing and burning fuel, and they exhibit necessary orientation and navigational skills. Avian migrants are still limited in the amount of time and energy they can allocate towards their movements and need to balance migration-related costs against expenditures associated with reproduction and maintenance. Different specialisations towards a migratory life will likely evolve depending on the ecology of the bird. My work aimed to investigate the ecology of large-scale movements of three species of aerial insectivorous birds by using miniaturised technology to record individual birds' position and activity during the non-breeding season. The common swift <i>Apus apus</i> and the pallid swift <i>A. pallidus</i>, are two highly aerial species that through their morphological and behavioural modifications are predisposed to a life in the air. Both species were documented to be air-borne throughout the non-breeding season which in the common swift results in a continuous flight for about ten months. Spending this time ranging over the African continent where large-scale weather systems generate an asynchronous seasonal landscape the swifts could potentially continuously track spatiotemporal variations in resources. However, the birds prioritised longer periods of residency briefly interrupted by shorter movement phases indicating that resource patchiness and local knowledge may be important determinants of the swifts' movement patterns.</p> <p>The crepuscular and nocturnal European nightjar <i>Caprimulgus europaeus</i> showed in contrast to the swifts a very limited activity pattern. It is a visual hunter that mainly forages during dusk and dawn, although on moonlit nights this temporal constraint is reduced. Throughout the non-breeding season I found a clear periodic pattern in both migratory flights and foraging activities suggesting that the European nightjar increased the migration speed by allocating the fuelling towards moonlit nights. Influenced by wind conditions en route, the tracked birds undertook loop-migrations where the spring routes were consistently west of autumn routes. The detoured routes were at least in spring beneficial for a migrant striving to reduce the amount of energy and time spent on migration due to an associated reduction in barrier crossing. This optimal detour varied with breeding longitude and resulted in a spatial linkage between the breeding site and the stopover locations associated with the barrier crossing. This indicates that any spatial variations in this important part of the annual cycle may influence population trends differently across the breeding population. Technical advances and miniaturisations of data-recording devices have enabled individual-based studies on more and more species and will likely reveal predicted as well as completely surprising examples of bird migrations in many years to come. In this thesis I have explored some of the large-scale movement patterns observed in a group of aerial insectivorous birds. Some of the results and conclusions reveal peculiarities of this specific group of birds while other findings, such as the selection of migratory routes, should be of a more general interest in the field of bird migration.</p>			
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- I. **Norevik, G.**, Åkesson, S. and Hedenström, A. 2017. Migration strategies and annual space-use in an Afro-Palaeartic aerial insectivore – the European nightjar *Caprimulgus europaeus*. *J. Avian Biol.* 48, 738-747.
- II. Hedenström, A., **Norevik, G.**, Warfvinge, K., Andersson, A., Bäckman, J. and Åkesson, S. 2016. Annual 10-month aerial life phase in the common swift *Apus apus*. *Curr. Biol.* 26, 3066-3070.
- III. Hedenström, A., **Norevik, G.**, Boano, G., Andersson, A., Bäckman, J. and Åkesson, S. 2018. Non-breeding flight activity in pallid swifts *Apus pallidus*. *J. Avian Biol. In revision*.
- IV. **Norevik, G.**, Boano, G., Hedenström, A., Lardelli, R., Liechti, F. and Åkesson, S. 2018. Highly mobile insectivorous swifts perform multiple intra-tropical migrations to exploit an asynchronous African phenology. *Oikos. In revision*.
- V. **Norevik, G.**, Boano, G., Hedenström, A., Lardelli, R. and Åkesson, S. Non-breeding space use in two aerial insectivorous birds: ecological isolation between common and pallid swifts during winter in West Africa. *Manuscript*.
- VI. **Norevik, G.**, Åkesson, S., Andersson, A., Artois, T., Bäckman, J., Beenaerts, N., Conway, G., Evens, R., Henderson, I. and Hedenström, A. Altitude selection and its association to environmental factors in a flapping flying avian migrant. *Manuscript*.
- VII. **Norevik, G.**, Åkesson, S., Artois, T., Beenaerts, N., Conway, G., Cresswell, B., Evens, R., Henderson, I., Jiguet F. and Hedenström, A. Wind-driven detours influence the seasonal migratory connectivity in a flapping flying long-distance migrant. *Manuscript*.
- VIII. **Norevik, G.**, Åkesson, S., Andersson, A., Bäckman, J. and Hedenström, A. Migration strategies in relation to topography and lunar cycle in European nightjars *Caprimulgus europaeus*. *Manuscript*.

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## Author contributions

- I. **GN**, **SÅ** and **AH** planned the study; **GN** conducted the field work; **GN** analysed data and drafted the manuscript with input from **SÅ** and **AH**.
- II. **AH** and **SÅ** conceived the study; **AA** and **JB** designed the micro data loggers and downloaded the data; **GN**, **AH** and **SÅ** conducted field work; **KW** simulated flight activity data; **AH**, **GN**, and **SÅ** analysed data; **AH** drafted the manuscript; all authors discussed the results and commented on the manuscript.
- III. **AH**, **SÅ** and **GN** conceived the study; **AA** and **JB** designed the micro data loggers and downloaded the data; **GB** conducted the field work; **AH**, **GN**, and **SÅ** analysed data; **AH** drafted the manuscript; all authors discussed the results and commented on the manuscript.
- IV. **GN**, **AH** and **SÅ** conceived the ideas; **GB**, **RL** and **FL** conducted field work; **GN** analysed data and led the writing of the manuscript with input from **AH** and **SÅ**; all authors discussed the results and commented on the manuscript.
- V. **GN**, **AH** and **SÅ** conceived the ideas; **GN**, **GB** and **RL** conducted field work; **GN** analysed data and led the writing of the manuscript with input from **AH** and **SÅ**; all authors discussed the results and commented on the manuscript.
- VI. **GN**, **SÅ** and **AH** planned the study; **AA** and **JB** designed the multi-sensor loggers and downloaded the data; **GN**, **GC**, **RE** and **IH** conducted field work; **GN** analysed data and drafted the manuscript with input from **SÅ** and **AH**; all authors discussed the results and commented on the manuscript.
- VII. **GN**, **SÅ**, **GC**, **RE**, **AH** and **IH** conceived the ideas; **GN** analysed data and drafted the manuscript with input from **SÅ** and **AH**; all authors discussed the results and commented on the manuscript.
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## Abstract

Many birds are predisposed to annually undertake movements over large temporal and spatial scales. They have an efficient flight machinery, demonstrate impressive capacities in storing and burning fuel, and they exhibit necessary orientation and navigational skills. Avian migrants are still limited in the amount of time and energy they can allocate towards their movements and need to balance migration-related costs against expenditures associated with reproduction and maintenance. Different specialisations towards a migratory life will likely evolve depending on the ecology of the bird. My work aimed to investigate the ecology of large-scale movements of three species of aerial insectivorous birds by using miniaturised technology to record individual birds' position and activity during the non-breeding season. The common swift *Apus apus* and the pallid swift *A. pallidus*, are two highly aerial species that through their morphological and behavioural modifications are predisposed to a life in the air. Both species were documented to be air-borne throughout the non-breeding season which in the common swift results in a continuous flight for about ten months. Spending this time ranging over the African continent where large-scale weather systems generate an asynchronous seasonal landscape the swifts could potentially continuously track spatiotemporal variations in resources. However, the birds prioritised longer periods of residency briefly interrupted by shorter movement phases indicating that resource patchiness and local knowledge may be important determinants of the swifts' movement patterns.

The crepuscular and nocturnal European nightjar *Caprimulgus europaeus* showed in contrast to the swifts a very limited activity pattern. It is a visual hunter that mainly forages during dusk and dawn, although on moonlit nights this temporal constraint is reduced. Throughout the non-breeding season I found a clear periodic pattern in both migratory flights and foraging activities suggesting that the European nightjar may strive to increase the migration speed by allocating the fuelling towards moonlit nights. Influenced by wind conditions *en route*, the tracked birds undertook loop-migrations where the spring routes were consistently west of autumn routes. The detoured routes were at least in spring beneficial for a migrant striving to reduce the amount of energy and time spent on migration due to an associated reduction in barrier crossing. This optimal detour varied with breeding longitude and resulted in a spatial linkage between the breeding site and the stopover locations associated with the barrier crossing. This indicates that any spatial variations in this important part of the annual cycle may influence population trends differently across the breeding population. Technical advances and miniaturisations of data-recording devices have enabled individual-based studies on more and more species and will likely reveal predicted as well as completely surprising examples of bird migrations in many years to come. In this

thesis I have explored some of the large-scale movement patterns observed in a group of aerial insectivorous birds. Some of the results and conclusions reveal peculiarities of this specific group of birds while other findings, such as the selection of migratory routes, should be of a more general interest in the field of bird migration.

## Svensk sammanfattning

Långdistansflyttande fåglar uppvisar ett flertal gemensamma egenskaper som ger dem goda förutsättningar att regelbundet förflytta sig över kontinentala avstånd. De har exempelvis en effektiv flygmotor som gör att de kan hålla sig flygande, och en god förmåga att både lägga på sig, och bränna fett som flygbränsle. Fåglar uppvisar i regel också goda orienterings- och navigationsegenskaper, vilket är en förutsättning för att kunna hitta vägen mellan häckningsplatserna och övervintringsområdena. Eftersom flyttfåglar behöver hinna med andra aktiviteter, som reproduktion och fjäderbyte, under året så är de fortfarande begränsade i mängden tid och energi de kan spendera under flyttningen. Beroende på fåglarnas levnadsätt och förutsättningar så kan man misstänka att anpassningen till ett liv som flyttfågel kan te sig olika mellan olika arter. Här har jag studerat de storskaliga rörelsemönstren hos en grupp fåglar som har specialiserat sig på att jaga luftburna insekter medan de själva flyger. Jag visar bland annat att tornseglare *Apus apus* och bleka tornseglare *A. pallidus* spenderar merparten av tiden utanför häckningsperioden i luften, vilket i tornseglarens fall kan innebära en flygtur på tio månader. Jag fann också tydliga samband mellan fåglarnas rörelser inom den Afrikanska kontinenten och de cykliska regnperioderna där de bleka tornseglarna systematiskt anlände till områden där regnen precis slutat. När jag jämförde rörelsemönstren hos samma bleka tornseglare med en grupp tornseglare så fann jag både några likheter och några skillnader. Tornseglarna anlände till övervintringsområdena söder om Sahara flera veckor tidigare än de bleka tornseglarna, men deras tidsförhållande till de undandragande regnen var slående lika eftersom tornseglarna stannade på platser norr om områdena senare använda av de bleka tornseglarna. I samband med de bleka tornseglarnas ankomst och med progressionen av torrsäsongen strax söder om Sahara så förflyttade sig tornseglarna söderut, förbi de bleka tornseglarna, och försköt därmed sitt temporära förhållande till regnsäsongen. De potentiella interaktionerna mellan de båda, påfallande lika arter, är spännande att spekulera i, fast deras storlek och rörlighet gör utforskningen av de bakomliggande mekanismerna till en utmaning. Trots att specialiseringen till ett liv i luften medför att de båda seglarna kan röra sig fritt över den Afrikanska kontinenten så håller de sig för det mesta på samma plats. Vid de få tillfällen seglarna rör sig över större avstånd förflyttar de sig till nästa rastplats, ett rörelsemönster förknippat med andra mer marklevande fåglar. Kanske är inte bara den potentiella kostnaden att växla mellan stationära och rörliga perioder viktig hos mobila arter, utan också faktorer som distributionen av föda och lokalkännedom för relativt långlivade arter som seglarna studerade här?

Nattskärnan *Caprimulgus europaeus* uppvisade tydliga ögleflyttningmönster där individernas flyttningvägar under våren konsekvent var lokaliserade väster om höstrutternas. Sådana mönster kan uppstå om förutsättningarna att lägga på sig

flygbränsle varierar geografiskt mellan höst och vår, eller om regelbundna storskaliga vindmönster förkortar resvägen längs vissa rutter beroende på den önskade flyttningsriktningen. Genom att ta hänsyn till förutsättningarna att flyga i medvind längs olika rutter över Saharaöknen kunde jag visa att flyttvägarna som nattskärorna använde överensstämde med de rutter där individen avväger förtjänsten att flyga i medvind över öknen och den adderade kostnaden att flyga en omväg. Tillsammans med observationerna att nattskärorna inte tycktes koncentrera sig vid enstaka lokaler söder om Sahara och att de svenska fåglarna överlappade sinsemellan i positionerna för vår- och höst-rastplatser, pekar resultaten på att vindförhållanden har en större inverkan än rastingshabitatet på nattskärornas flygvägar.

Utänför häckningssäsongen var nattskärorna framförallt aktiva i gryningen och skymningen samtidigt som vi fann tydliga samband mellan fåglarnas aktiviteter och måncykeln. Eftersom nattskärorna använder synen under jakten på insekter så är den sannolikt begränsad till perioder med relativt goda ljusförutsättningar. Givet detta samband kan nattskärorna påskynda sin flyttning genom att lägga på sig bränsle under månljusa nätter och flytta när förutsättningarna blir sämre. Efter att ha analyserat data på nattskärornas flyttning över flera år, kunde vi konstatera att det så var fallet. En intressant aspekt rörande sambandet mellan flyttningen och månfaserna är att måncykeln förskjuts mellan åren, vilket sannolikt påverkar fåglarnas ankomsttid till t.ex. häckplatsen. Med tanke på att det finns många arter vars dagliga födosöksförutsättningar skulle kunna påverkas av periodiciteten i måncykeln öppnar det upp för nya frågor för hur flyttfåglar hanterar sådana förutsättningar på ett optimalt sätt och jag hoppas det inspirerar framtida teoretiska och empiriska undersökningar.

Miniatyriseringen av data-loggar som man kan montera på friflygande fåglar har öppnat upp oanade möjligheter att studera migrationen hos allt mindre fågelarter, och möjliggjort tester av hypoteser såväl som beskrivande analyser av flyttningsmönster. I den här avhandlingen har jag undersökt några av de storskaliga rörelsemönster hos några fågelarter som fångar insekter i luften. Några av mina resultat och slutsatser rör egenheter hos denna specifika grupp fåglar. Samtidigt har jag studerat frågor som kan vara av ett mer allmänt intresse hos flyttfågelforskare, som exempelvis utformningen av nattskärornas flyttvägar.



# Background

In this thesis I have utilized ecological and theoretical knowledge about bird migration to pose and hopefully answer questions regarding movements over large spatial and temporal scales, such as the seasonal migrations between temperate breeding areas and tropical non-breeding ranges. The thesis focuses on a group of long-distance migrating land-birds within the Palaearctic-African migration system specialised in feeding on aerial prey. The results presented here are mainly derived by using individual-based tracking techniques at the frontline of development. In order to put my results in an ecological and evolutionary context I have applied a comparative approach where the recorded movement patterns are contrasted within and between individuals. Alternatively, I have contrasted my results against predicted outcomes if the birds behaved according to different optimality criteria, such as maximising safety or minimising energy or overall time spent on migratory movements.

## Scales for studying moving animals

The capacity to move enables animals to respond to external factors, resource abundance and competition by relocating into areas with improved conditions for survival or reproduction (Dingle 1996). The resulting movement patterns likely differ depending on the scale at which they are observed and documented, as the level of detail will vary if the recording sampling rate is one hour, one day or one month, but also because the different proximate factors influencing movement will act upon the animal on different scales (Levin 1992; Fryxell et al. 2008). On a daily basis response to short-term needs, such as fuelling, resting and safety are likely met by performing relatively small-scale movements within a restricted area (Fryxell et al. 2008). On an annual time-scale, animal movements generally correlate with the seasonality of the environment and the associated fluctuations in food resources (Yang et al. 2008; Armstrong et al. 2016; Thorup et al. 2017). In this thesis the focus will be on the larger scales although I have visited questions regarding daily activities when they relate to the movement patterns observed across migratory seasons and between regions.

## Adapted to fly

Many birds show characteristics needed for being flyers (Norberg 1990); they have an advanced respiratory system that allows for efficient oxygen uptake, and their reduced bone structure lowers body weight, thus making it less costly to stay air-borne. Further, most birds have an ability to store energy that later can be used during especially demanding periods (such as long flights) and they have a complex and highly efficient flight apparatus (Jenni and Schaub 2003; Leisler and Winkler 2003). Both migratory and non-migratory birds have demonstrated endogenous rhythms that can function as regulators of activities within the annual cycle (e.g. Gwinner 1990; Helm 2006). Regardless of whether they are adaptations or pre-adaptations for large-scale aerial movements, we can analyse traits related to avian flight and migration to explore how natural selection has acted on these traits to modify and maintain adaptations in the bird's ecological context (Åkesson and Hedenström 2007; Salewski and Bruderer 2007). As migration speed is determined by a combination of internal factors (Alerstam and Lindström 1990, Alerstam et al. 2003), related to the bird's physiology, morphology, and behavioural responses to environmental variables I will briefly introduce some of them below.

### Physiology

A self-powered flapping flying bird needs to fuel in an efficient manner to afford the high cost of a working flight apparatus (Norberg 1990). The capacity in foraging and metabolizing foodstuffs scales with the animal's basal metabolic rate (BMR), and has been observed to be maximized at around four times BMR (Drent and Daan 1980; Kirkwood 1983; Lindström and Kvist 1995). This indicates that when food is plentiful, birds will approach their metabolic ceiling and assimilation rate will be the factor ultimately limiting daily fuelling and hence the overall speed of migration (Lindström 1991; Hammond and Diamond 1997).

After assimilated energy has been allocated towards basal metabolic needs, thermoregulation and locomotion, the excess may be stored for future costs such as migratory flights (Jenni and Jenni-Eiermann 1998; Guglielmo 2018). On a daily basis, the rate at which fuel is added may correlate with the amount of time available for foraging, and daily fuelling rates have the potential to determine migration speed (Kvist and Lindström 2000). Hence, since basic physiological features can set a limit on the rate at which energy can be gained; morphological modifications reducing energy expenditure during flight should have a high adaptive value in energy- and time-minimizing migrants (Pennycuick 1975; Alerstam and Lindström 1990; Hedenström and Alerstam 1997).

## Morphology

Self-powered flapping flight is a fast locomotion mode, but it is also relatively energy expensive (Schmidt-Nielsen 1972). Active flyers generate a combination of forward thrust and upward lift by flapping their wings (Norberg 1990). With increased forward speed an aerodynamic force by the wing profile generates additional lift. To overcome drag experienced while flying, the bird needs to flap their wings to generate a thrust from the flight apparatus. Lift-dependent drag is a result from the downwash when creating lift and the parasitic drag is the combined effect of air friction and pressure drag from the body and wings (Pennycuick 1975). An increased forward speed thus generates more lift from the wings, which can balance a larger body mass, but a higher speed also results in a steep increase in overall drag and power required to fly (Norberg 1990).

The resulting U-shaped relationship between air speed and power spent on flapping flight suggests that birds in endurance flight will operate in a small speed range relative to their maximum capacity (Pennycuick 1975). It also predicts that active fliers should modulate air speed slightly depending on whether they strive to fly for as long time, or as far as possible on a certain amount fuel (Hedenström and Ålerstam 1997). Mean flight speeds in the common swift have for example been documented to be  $9.0 \text{ ms}^{-1}$  during aerial summer roosts and  $10.6 \text{ ms}^{-1}$  during spring migration although the species is capable to reach speeds of  $31.1 \text{ ms}^{-1}$  during horizontal burst flights (Henningsson et al. 2009, 2010). The shape of the curve, and thus the precise nature of the power – speed relationship will largely depend on aerodynamic characteristics of the animal (Pennycuick 1975). Hence, active flyers spending long periods of time in the air would benefit through reductions of energy expenditures by morphological modifications (Norberg 1990). Migrants have been shown to have relatively longer and slender wings (Mönkkönen et al. 1995), which is a characteristics predicted to reduce energy costs in forward flight (Rayner 1988).

The relationship between weight and flight costs has consequences for how birds with different migratory strategies are expected to organize migration, as the power needed to stay airborne will increase with each added gram of fuel (Pennycuick 1975; Hedenström and Ålerstam 1997). The negatively accelerated relationship between fuel load and potential flight distance suggests that energy-minimizing migrants may even strive to use routes longer than the shortest one if it allows for movements with smaller fuel loads (Ålerstam 2001).

## Behaviour

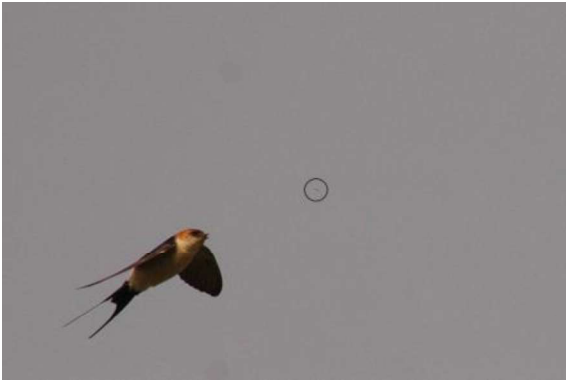
Except for morphological and physiological modifications toward a mobile lifestyle, migrating animals have acquired a suit of behavioural characteristics related to large-scale movements (Åkesson and Hedenström 2007). Avian migrants need to respond correctly to external cues that guide them to initiate the migration timely, to fuel properly (but not too much) for subsequent flights, and to be able to orient themselves towards a distant goal (Gwinner 1990; Lind et al. 1999; Fransson et al. 2001; Åkesson et al. 2017).

While airborne, flying animals move through a highly dynamic and variable medium (Dingle 1996; Gautheraux 2005; Liechti and McGuire 2017; Shamoun-Baranes et al. 2017). As winds regularly operate at similar speed as the birds' own air-speed, the resulting ground distance of the flying bird could be double or completely impeded, depending on the alignment between the birds' intended flight direction and the movement of the surrounding air (Liechti and Bruderer 1998). An ability to evaluate and accordingly respond to wind conditions would thus provide a fitness advantage by allowing for a safer and more time- and energy efficient migration. Birds generally behave as expected and take off, adjust flight altitude and abort flights depending on current air-flow (Alerstam 1979; Richardson 1990; Gautheraux 1991; Schmaljohann et al. 2009). However, details on how individual small birds behave in-flight during long-distance movements are still scarce.

## Aerial insectivorous birds

Birds predominantly foraging on flying insect prey are broadly defined as aerial insectivores (Figure 1), although there are some general differences in the specific hunting approaches. Some species such as swifts search, hunt, and catch their prey as they fly, while a hawking strategy likely is more common among for example nightjars (Cramp 1985).

The large amount of time spent on the wings suggests that this group of species may face a relatively strong selective pressure towards an energy-efficient flight, which is indicated by the relatively low flight costs (Guglielmo 2018). The two swift species and the European nightjar that are in focus in the present work have adopted rather different lifestyles although they all are aerial insectivores (Figure 2). Broadly the swifts show a relatively high preference to roam the open air-space, while the nightjar is known for its crepuscular and nocturnal lifestyle, and for the habit of spending the daylight hours quiescent (Cramp 1985). The contrasting strategies in daily movement patterns have the potential to translate into different specialisations and constraints affecting the large-scale movements within the annual cycle, which I have aimed to investigate in this thesis.



**Figure 1 Representative images of aerial insectivorous birds**

Left: A red-rumped swallow *Cecropis daurica* about to catch a prey (encircled) mid-air. Right: An about three week old European nightjar *Caprimulgus europaeus* demonstrating its impressive gape size that is likely an efficient tool when catching a mobile prey while flying. Photos: Gabriel Norevik.

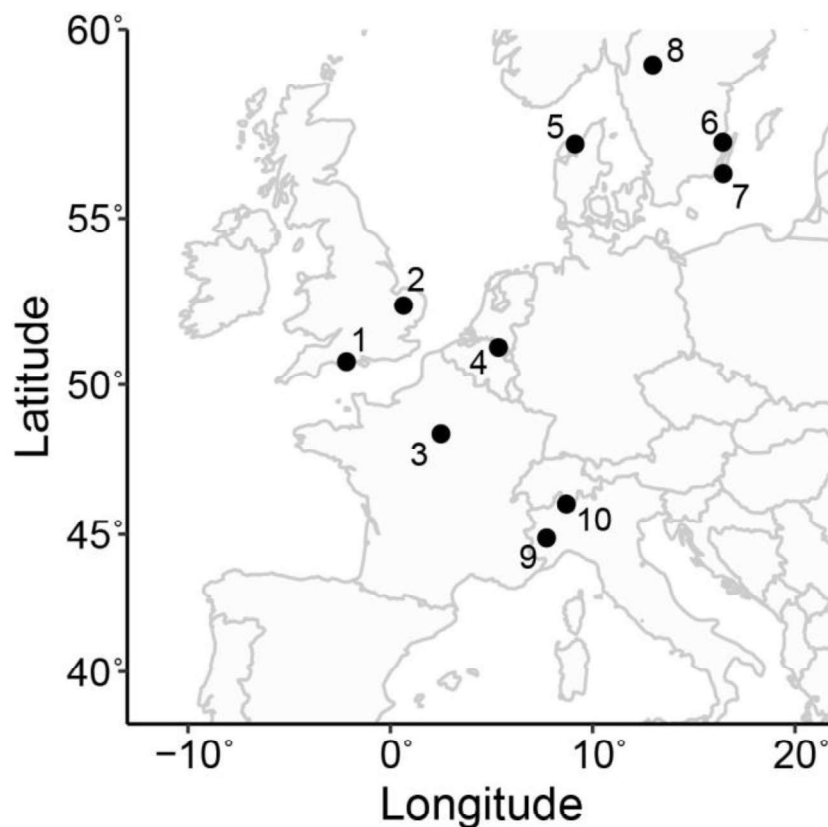


**Figure 2 The study species in their natural settings**

Upper and lower left: A pallid swift *Apus pallidus* and a common swift *A. apus* demonstrating their similar morphology with long, slender wings and streamlined bodies. Upper and lower right: European nightjars *Caprimulgus europaeus* being predominately active around dusk and dawn while spending the daylight hours motionless. Photos: Upper right: Urban Rundström; the rest: Gabriel Norevik.

# Aims and study sites

This thesis aimed to investigate the ecology of movement activities over large temporal and spatial scales in birds that hunt insect prey on their wings, focusing on long-distance migrating *Apus* and *Caprimulgus* species (Cramp 1985). Common for all studies is the use of individual-based miniaturized devices that collect and store data about the location (sometimes including altitude) and activity as reflected by the wingbeat pattern. Depending on the questions in focus, different types of devices were used in different studies. In some cases more than one variable were recorded simultaneously by multi-sensor loggers and in two studies a combination of devices have been used. An overview of the different study site locations is presented in Figure 3.



**Figure 3 Locations of tag deployments**

An overview of the distribution of the European sites involved in the different studies presented in the thesis. Some closely neighbouring sites have been merged to facilitate visualization.

In **Paper I** we studied the migration strategies and annual space use in European nightjars tracked from breeding areas in southern Sweden (sites 6 and 7; Figure 3) using geolocators. The distribution of migratory routes as described by stationary sites was evaluated to explore potential seasonally related patterns.

In **Paper II** we studied the non-breeding movement activity in common swifts from two colonies in Sweden (sites 7 and 8; Figure 3) to test the hypothesis that common swifts are airborne throughout the non-breeding season.

In **Paper III** we studied the non-breeding movement activity in pallid swifts from colonies in Italy and Switzerland (sites 9 and 10; Figure 3) to test the hypothesis that the pallid swift also exhibit the aerial behaviours observed in the common swifts.

In **Paper IV** we aimed to analyse the large-scale non-breeding movements of pallid swifts from sites 9 and 10 (Figure 3), and explore the potential associations with local environmental factors related to the seasonal phenology within the northern sub-Saharan Africa. We hypothesised that the pallid swifts regularly would improve their habitat by moving as conditions deteriorate and that the timing of these movements should be related to important changes of the habitat quality in both departure and arrival sites.

In **Paper V** we aimed to investigate the spatial and temporal aspects of the sub-Saharan non-breeding distribution of common swifts from site 8 (Figure 3), and to relate the birds' movements to the local seasonality following the procedure in **Paper IV**. Pallid swifts generally spend longer time in the breeding area, and consequently arrive later to sub-Saharan Africa. We therefore contrasted the space- and niche-use of common swifts before and after the mean arrival of the pallid swifts (tracked in **Paper IV**), to investigate any potential overlap in range use (i.e. direct or indirect competition) between the two species.

In **Paper VI** we investigated the ranges of altitudes used by migrating European nightjars from sites 1, 4 and 6 (Figure 3) and how altitude selection varied with regions. We explored the association with environmental variables previously described to relate to migrants' altitude distribution. We studied the altitudinal profiles of the birds' flights and tested hypotheses based on the propositions that birds explore the air-column during the early night before settling at a lower altitude during the cruising period of the flight.

In **Paper VII** we examined the extent and potential causes of detours and seasonal migratory connectivity in European nightjars tracked from breeding sites along a longitudinal gradient (sites 1-7; Figure 3) mainly using data from geolocators. We aimed to quantify the degree of spatial relationship between different important stationary sites within the annual cycle (i.e. breeding and main non-breeding sites, and the stopovers just south of the Sahara desert). Under the prediction that nightjars strive to minimise the energy expenditure associated with the barrier crossing, we tested if the benefits from the quantified barrier reduction outweighed the cost of the added distance along the detoured routes.

In **Paper VIII** we studied migration strategies in European nightjars tracked from southern Sweden (site 6; Figure 3) aiming to link daily behaviours to seasonal and annual movement characteristics, and to explore the potential relationship with the lunar cycle. We used the GPS data to provide a general overview of the distribution of the birds across the annual cycle, and to test if daily travel speeds differed between seasons and larger regions (Europe, Sahara, and sub-Saharan Africa). We documented the daily timing of activity of the birds using flight activity measurements recorded by multi-sensor loggers and tested the hypothesis that European nightjars are strictly crepuscular and nocturnal throughout the annual cycle. We calculated the daily flight duration to test if the birds allocated more time on migratory flights over the Sahara desert than in Europe, and to evaluate their time allocation within sub-Saharan Africa. Under the prediction that moon light influences the foraging opportunity in a nocturnal visual hunter we tested the temporal relationship between lunar cycle and migration pattern of European nightjars.



# General methodology

## Trapping and handling of birds

All fieldwork was undertaken at sites within the breeding range of the study species. Birds were trapped in association with the breeding colonies (swifts) or within their presumed breeding areas (nightjars), mainly using mistnets (Figure 4).



**Figure 4 Commonly used trapping configurations when targeting the swifts and European nightjars**  
Left: Common swifts *Apus apus* regularly breed under the roof of old farm houses in central Sweden. The birds were trapped as they left their nests after the night roost. Right: European nightjars *Caprimulgus europaeus* trapped in managed pine forests an early morning in southern Sweden using playback lure. Photos: Gabriel Norevik.

Trapped individuals were ringed, or controlled if already ringed, determined as to sex (nightjars) and age. We recorded wing length (max length flattened chord: Svensson 1992) to the nearest mm using a ruler, and body mass to the nearest 0.1 g using an electronic balance, and photo documentation of the extent of wing feather moult. A subset of birds was equipped with archival tags of types that

varied depending on species and study aims (Figure 5). Study sites were regularly visited in subsequent breeding seasons with the aim to relocate and recapture the tagged individuals.



**Figure 5 Tag deployment**

All tags were deployed using a full-body harness placing the tag dorsally between the wings. A common swift *Apus apus* (left), and a European nightjar *Caprimulgus europaeus* (right) with newly mounted archival GPS tags illustrating placement of tags on the study species. Photos: Gabriel Norevik.

## Device types and sampling routines

Various types of devices were used depending on the study species, aim of the study and the development timing of the device types. Initial studies on the three species used geolocators (Åkesson et al. 2012; Norevik et al. 2017, 2018, **Papers I, III**), and more specific follow-up studies have used archival GPS-tags, and custom made multi-sensor loggers primarily developed to monitoring the flight activity of the study objects by sampling wing-beat derived variations in vertical acceleration. Auxiliary measurements recorded by the multi-sensor loggers involve periods of sampling of light data for geolocation and an hourly registration of barometric air pressure, which were translated into approximate altitudes by using standardized atmospheric calculations. For further details about the procedure to derive approximate altitudes from ambient air pressure, consult **Papers III** and **VI** and their respective supplementary files.

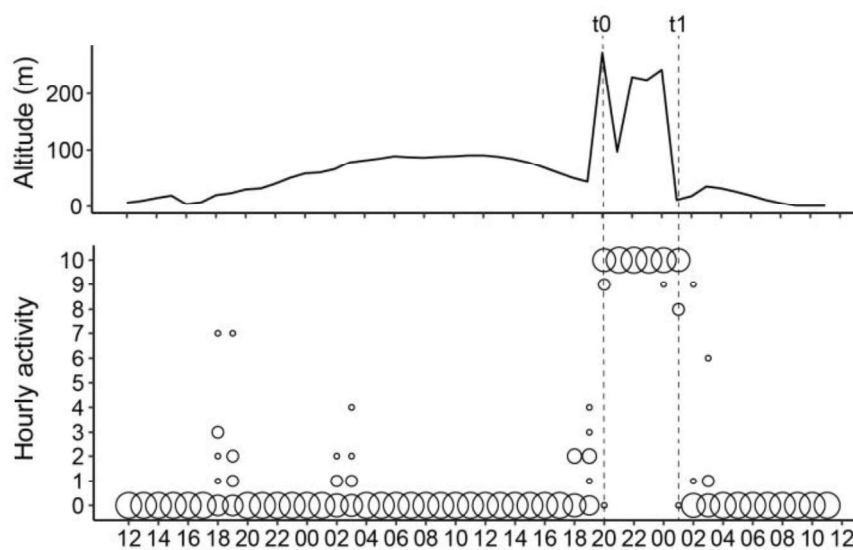
## Data handling

We consistently used the threshold-based method to translate light data recorded by the geolocators into geographical positions (Hill 1994; Hill and Braun 2001). This is a simple approach determining the timing of the transitions between day and night by using a specific light value as a threshold, and does not require data

sets of full light-ranges or a calibration period to determine the sun-angle for the threshold light-level. For the swifts we applied a “Hill-Ekstrom” calibration on the geolocation data as the birds consistently roosted in their nest cavities at dusk and dawn making an on-board calibration impossible (Ekstrom 2004). For the European nightjars (**Paper I**), we used both calibrations to evaluate the coherence of the two approaches.

In **Papers II, III, VI and VIII** we used custom built multi-sensor loggers. The first versions were primarily used to record flight activity of individual bird by sampling the wingbeat-generated acceleration (**Paper II**). Additional sensors have later been included to provide estimates of the location and altitude of the bird. In Figure 6 is an example of a time series of altitude data derived from barometric pressure measurements and corresponding activity recordings. The dashed vertical lines show the timing of a migratory flight and illustrate how the two sampling routines provide independent information about the timing of flight by the deployed bird.

Different environmental variables were annotated to the tracking data depending on the specific questions. Environmental data were either sampled based on the timing and position of each location, or by downloading series of snapshots of data over larger geographical areas to construct time series, used for analyses of phenology.



**Figure 6 Activity and altitude data from multi-sensor loggers**

Hourly summaries of activity (bottom) and measurements barometric-based altitudes (top) sampled by a multi-sensor logger during a period of two days, starting and ending at noon. Circle size corresponds to the number of registrations observed per hour (1-12). An extended period of flight activity is initiated during hour 20 the second night ( $t_0$ ) resulting in a relatively large and rapid increase in altitude. At hour 01, ( $t_1$ ) the first low activity registration occurs and the altitude has dropped and continues to be relatively stable throughout the rest of the night. This translates into a core period of 4 hours (21-00). As there are 11 registrations of high activity levels and only one registration of a low activity level both in the preceding hour (20) and the following hour (01), 55 minutes are added in both ends of the core period resulting in an approximated flight segment of 5 hour and 50 minutes. Note that in both the first and the second night there are a number of registrations of intermediate activity levels in the evening and morning, which likely are associated with foraging events. Also note how the altitude estimate gradually changes over the day as the sampled barometric pressure vary, likely due to e.g. a passage of a low-pressure system. From **Paper VIII**.



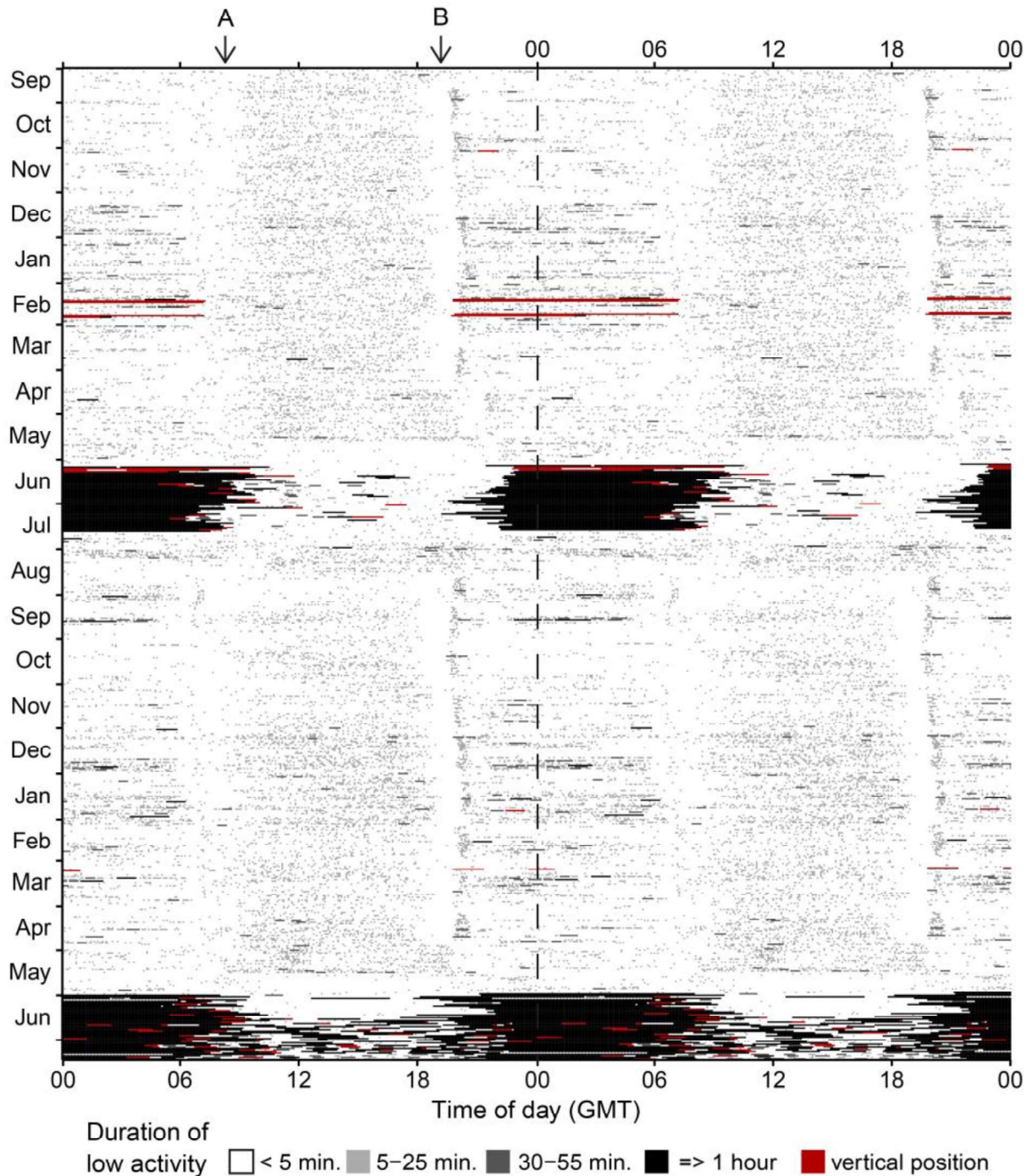
# Combining flying and foraging

## What limits the movement potential?

Flight is a relatively energy expensive but fast locomotion mode and it is often among the small avian migrants we find the longest migration distances (Alerstam et al. 2003; Hedenström 2006; Bridge et al. 2011; Sokolovskis et al. 2018). In self-powered flapping-flying birds the power required to stay air-borne is generally several times higher than the rate of which fuel can be processed, forcing them to rely on endogenous energy stores to power the flight (Jenni and Jenni-Eiermann 1998; Guglielmo 2018). Migration by means of flapping flight therefore requires a preparation period during which the fuel for the movement is stored. In birds performing continental-wide flights of thousands of kilometres the fuelling period may take several weeks (Gill et al. 2009; Klaassen et al. 2010). Using cost estimates of flight, and maintenance at stopovers, Hedenström and Alerstam (1997) calculated the approximate relationship of total energy, and time expenditure between stopovers and flight for small to medium-sized birds to be 2:1 and 7:1 respectively, suggesting that only a third of the energy and about 12 % of the time is spent on the actual movement. Both the energy relationship (Wikelski et al. 2003) and the flight fraction have been quantified empirically in a few cases, resulting in values close to predictions (Hedenström et al. 2013; Norevik et al. 2017; Sokolovskis et al. 2018, **Paper I**).

## The occurrence of continuous flights

Some species however, like the great frigate bird *Frigata minor* (Weimerskirch et al. 2016) and three species of swifts *Apus ssp.* (Liechti et al. 2013; Hedenström et al. 2016, 2018, **Papers II, III**), have been documented to regularly undertake months-long flights, and thus appear to be revealed from the long preparation periods on ground seen in other birds. The common swift, reported to be air-borne for up to 10 months throughout the non-breeding season currently holds the record of endurance flight (**Paper II**; Figure 7).



**Figure 7 Flight activity in a common swift *Apus apus***

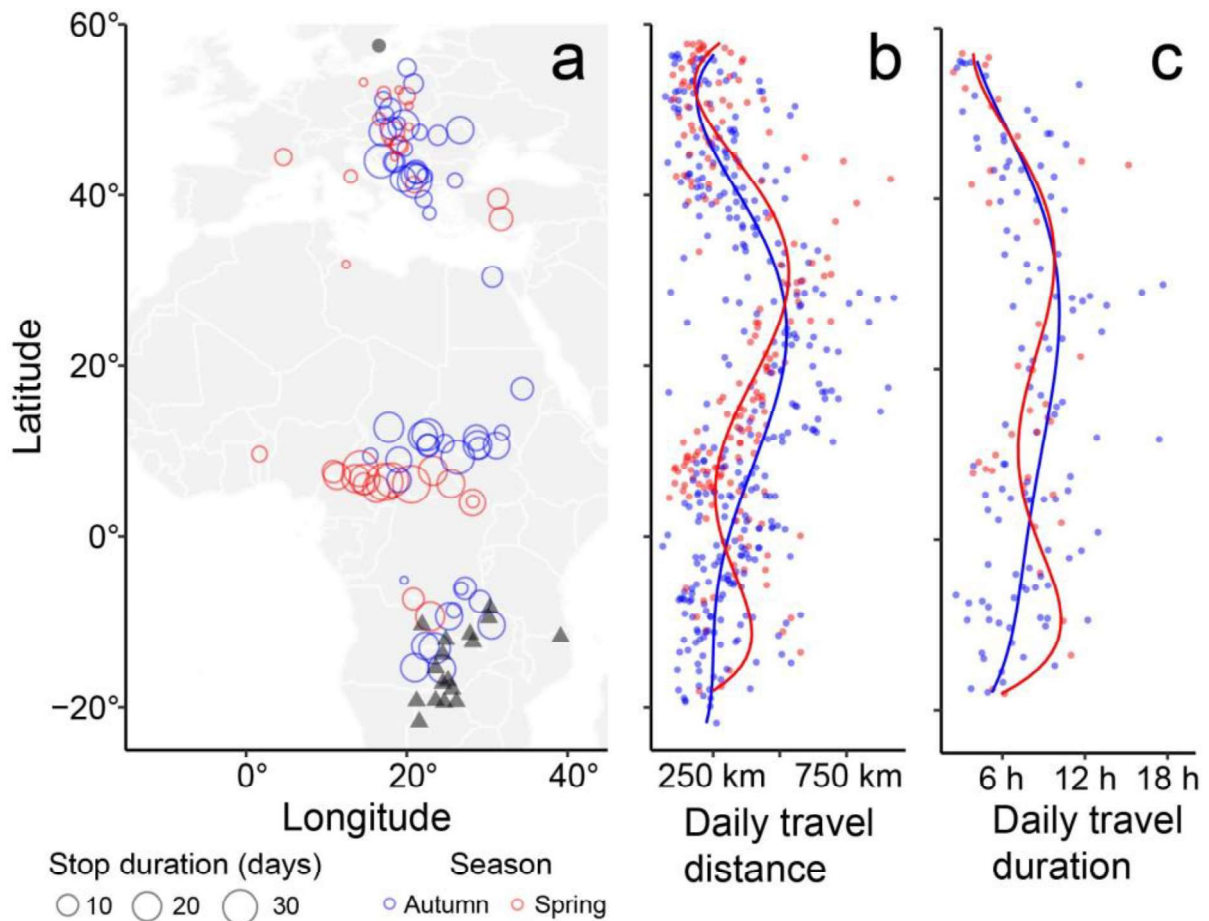
Flight activity diagram showing flight activity for a common swift during two successive years 2013-2015 recorded by the first version of multi data loggers. Each horizontal line shows accelerometer data from two consecutive days, where the second day is duplicated as the first day on the next line. Black horizontal bars show recordings indicative of non-flight, which in most cases are false indications due to the species' flap-gliding flight style. Red horizontal bars indicate that the bird's body orientation is near vertical, which means it is not flying. In the summer the activity pattern show alternate periods of foraging and nest visits. Arrows at the top indicate flight activity peaks around (A) dawn and (B) dusk, respectively. From **Paper II**, reprinted with permission from the publisher.

Probably these swifts have managed to reduce the energy expenditure related to flight to such degree that it is continuously balanced by the food collected and processed. The well-studied common swift demonstrates a suit of physiological and morphological modifications that presumably has led to an energy efficient flight such as high-aspect ratio wings, streamlined body and an energy-saving flap-gliding flight style (Henningsson et al. 2008; Lentink et al. 2007; Muijres et al. 2012; Sachs 2017), which is shared by the similar Alpine and pallid swifts. Provisional calculations based on the energy expenditures in flight and non-flight indicate that the pallid and common swift, due to their low-cost flight, have approached annual energy budgets corresponding to similar-sized but more terrestrial avian migrants (**Paper III**).

## Time allocation during migration

A specialisation of the ability to power the movement by foraging in mid-air and to extract potential energy from up-winds is likely a prerequisite for a continuous flight to evolve (Weimerskirch et al. 2016; Hedenström et al. 2016, 2018, **Papers II, III**). But a migration strategy integrating flying and foraging could be advantageous under certain conditions also for mainly terrestrial birds. By using a fly-and-forage migration strategy birds may reduce the costs associated with the time and energy spent on finding and establishing themselves at a stopover site (Rappole and Warner 1976), although it presumably comes with the cost of a reduced travel speed as potential flight time is allocated towards foraging (Strandberg and Alerstam 2007). In addition, it is likely a necessity that food is rather evenly distributed and that its abundance is possible to evaluate by migrants *en route*. Aerial insectivorous birds thus seem to be predisposed to apply a fly-and-forage strategy as they in theory should be able to sample their prey density as they move across the landscape.

The European nightjars showed higher daily travel speeds over the Sahara than in Europe, a pattern partly associated with the allocation of available time towards active flight (**Paper VIII**; Figure 8). Investigations on time allocation in Palaearctic-African migrating raptors reveal a similar result in ospreys *Pandion haliaetus*, but the pattern was less clear in the Montagu's harrier *Circus pygargus* (Klaassen et al. 2008, 2017). The pattern seen in the European nightjars and the ospreys indicates that they, at least on a daily basis, may mix migration with foraging events and that at least the search and settling phase of the foraging could be undertaken while moving in the migratory direction as have been shown in the osprey (Strandberg and Alerstam 2007).



**Figure 8 Distribution and daily flight characteristics in non-breeding European nightjars**

Stationary periods longer than two days were mainly distributed in East Europe, just south of the Sahara desert and within the southern Tropics. Spring locations just south of Sahara were west of the autumn sites resulting in a clockwise loop-migration pattern over northern Africa. b) the daily travel distance varied across latitudes in both autumn and spring being largest in latitudes associated with the crossing of the Sahara desert and the Mediterranean Sea, and lower in more benign regions, recognised by the long stationary periods. c) the estimated daily travel duration show that the rare cases when daily time spent on migratory flight exceed 12 hours are associated with the crossing of the Sahara desert and the Mediterranean Sea. Lines in fig b and c are polynomial regressions. Daily travel distances and travel durations are superficially similar across latitudes with the differences found just south of the Sahara desert, where spring values generally are lower, and in the sub-Saharan Africa, where autumn values are lower. From **Paper VIII**.

Similarly to what recently have been observed in other Palaearctic-African avian migrants (Adamík et al. 2016; Ouwenhand and Both 2016; Bäckman et al. 2017), we found occasions when individual nightjars extended their migratory flights into the daylight hours during the desert crossing (**Paper VIII**). This indicates that the birds did strive to speed up the daily movement across this relatively inhospitable region. However, congruent with radar-based studies on avian migration over the Sahara (Biebach et al. 2000; Schmaljohann et al 2007; Figure 13), nightjars were for most of the time strictly nocturnal while resting in the desert during daylight hours.



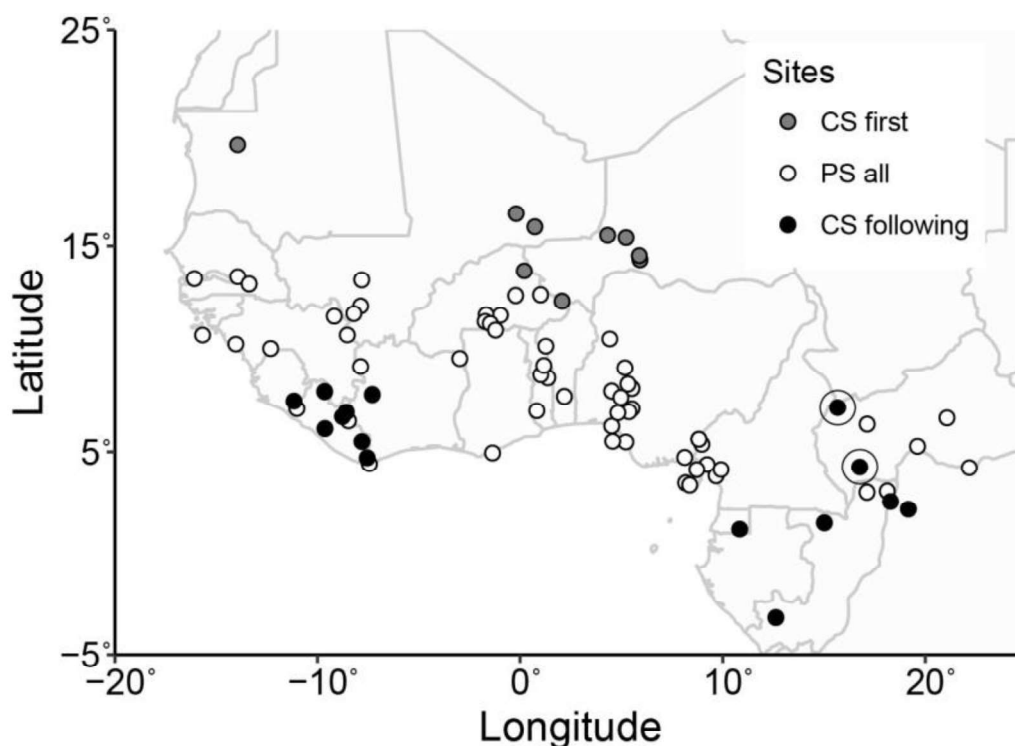
# Wintering in a seasonal landscape

It has long been recognised that the environment that meets the Palaearctic migrants upon their arrival to the sub-Saharan Africa is far from static (Moreau 1972; Morel 1973; Curry-Lindahl 1981; Jones 1996). Similar to how the amount of daylight hours and ambient temperature dictate the living conditions in the temperate regions, the periodic variation in precipitation is a large-scale regulator of the primary productivity on the African continent (Alerstam 1990). The Intertropical Convergence Zone (ITCZ), a large belt of convective air-masses where dry air from the Sahara desert meet wet air-masses from the Atlantic, resulting in the Intertropical Front, which generates the main rains in Western Africa (Waliser and Gautier 1993; Nicholson 2012). While tracking the zenith of the sun, the ITCZ moves back and forth around the equator, and is located at its northernmost point during the northern summer. As the tropical migrants leave the breeding areas in late summer they timely arrive to regions in northern sub-Saharan Africa as when the environment is still lush and food are relatively abundant (Moreau 1972; Morel 1973; Bensch et al. 1991; Jones 1996). Soon, as the rains move south, the conditions deteriorate and will remain poor until the next rainy season several months later (Waliser and Gautier 1993; Nicholson 2012). Many migrants respond to the deteriorating conditions by resuming their migration and follow the withdrawing rains southward (Jones 1996).

## The ecology of intra-tropical migrations

The large-scale movements often referred to intra-tropical migrations (Stutchbury et al. 2016), has long been recognised by ornithologists studying the avian fauna on the African continent and visitors to the bird ringing lodge at Ngulia in the Kenyan highlands may witness high numbers of migrating birds far outside the regular migration period (Pearson and Backhurst 1976; Curry-Lindahl 1981). There are ample studies describing the association between the local seasonality and the passage of Palaearctic migrants (e. g. Dingle and Khamala 1972; Lack 1983), and with individual-based tracking it is now possible to investigate how individuals respond to the local seasonality. By being continuously in the air (Hedenström et al. 2016, 2018, **Papers II, III**) common swifts and pallid swifts

should be predisposed to closely track the seasonality in the landscape and truly surf a resource wave following the withdrawal of the rains (Yang et al. 2008; Armstrong et al. 2016). Although some individual pallid swifts used several residence sites in comparison to other long-distance migrants (**Paper VI**; McKinnon et al. 2013) the two swift species mainly exhibit (on a sub-continental scale) long stationary periods within sub-Saharan Africa interrupted by shorter phases of more direct movements (Åkesson et al. 2012; **Papers VI, V**; Figure 9). Apparently also for species able to freely range the air-space a life centred to a sequence of residence sites may be superior to a true nomadic movement strategy (Jonzén et al. 2011). There are likely topographic features and wind patterns that influence the spatial distribution of aerial prey resulting in local food concentrations exploited by the swifts.



**Figure 9 Stationary sites of temperate-breeding swifts wintering in sub-Sahara**

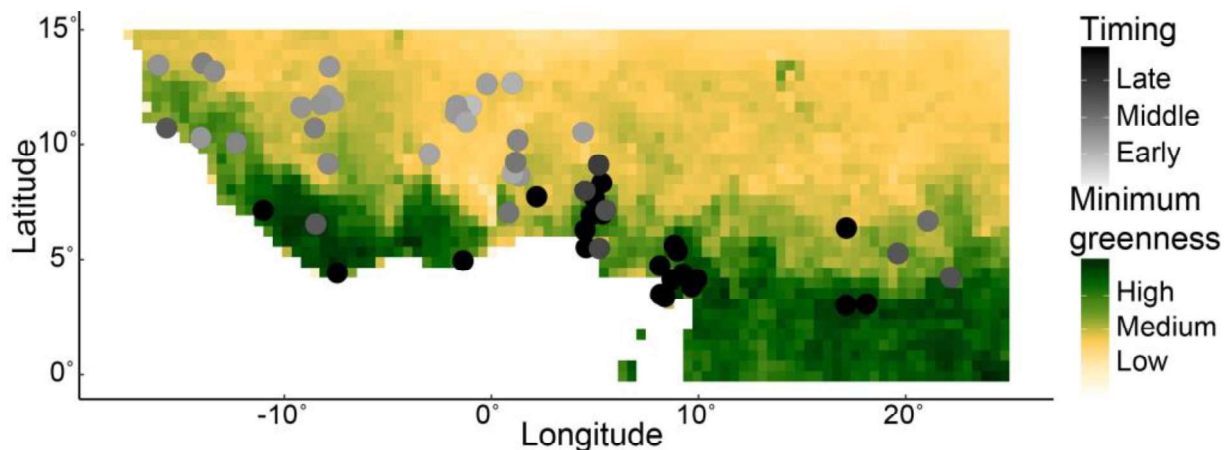
Distribution of stationary sites in northern sub-Sahara up to the peak of dry season (1 February). White dots correspond to all sites used by pallid swifts *Apus pallidus* (PS), while grey and black dots refer to first and consecutive sites used by common swifts *A. apus* (CS), respectively. Encircled black dots represent sites used *en route* by the two common swifts that used more than two residence sites (see main text). From **Paper V**.

Movements of common swifts within the breeding range have been related to both see-breeze fronts and low-pressure systems and, potentially, such movements can reveal details of weather-related movement strategies of swifts also within the non-breeding range (Koskimies 1947; Lack 1955; Simpson 1967). In addition, given that aerial prey is non-randomly distributed, a prior experience of an area likely provides a competitive advantage to individuals being naïve to their

environment (Wolf et al. 2009). Site fidelity between seasons appears to be rather common in migratory animals and may have a large influence on their movement patterns (Cresswell 2014). We still await a large-scale study on the site fidelity between seasons in swifts, but a study presenting repeated annual tracks of three individual common swifts provisionally suggests that site fidelity is relatively high also between years (Wellbrock et al. 2017). These observations support the indications that a patchy prey distribution and the relative advantage of a local experience (Wolf et al. 2009; Blackburn and Cresswell 2016) influence the spatiotemporal distribution of individual swifts wintering in Africa.

## Tracking resource waves

The arid landscape in West Africa shows both seasonal and inter-annual variability in the duration of the rainy season likely affecting the local phenology within the non-breeding range of pallid swifts (Nicholson 2012; **Paper IV**; Figure 10). So, if the swifts are faithful to their residence sites, they will need to adjust their temporal setting in order to match the spatiotemporal habitat phenology. We learned from **Paper IV** that individual pallid swifts made use of the asynchronous phenology within their non-breeding range by performing movements towards lush areas, which is similar to what have been reported in studies of other tracked Palaeartic-African migrants (Trierweiler et al. 2013; Thorup et al. 2017; Koleček et al 2018; Figure 10).



**Figure 10** Intratropical migrations in relation to local phenology in West Africa

Graphical representation of the relative minimum annual greenness showing the geographic distribution of highly vegetative and relatively lush areas, overlaid with the residence areas of the pallid swifts *Apus pallidus* colour coded by the relative timing of the birds' visits. As the season progresses the pallid swifts move to successively lush areas and spend the driest part of the non-breeding period in the greenest areas. Due to their location, these areas have the shortest annual dry season and thus provide relatively high abundance of food when conditions deteriorate further to the north. From **Paper IV**.

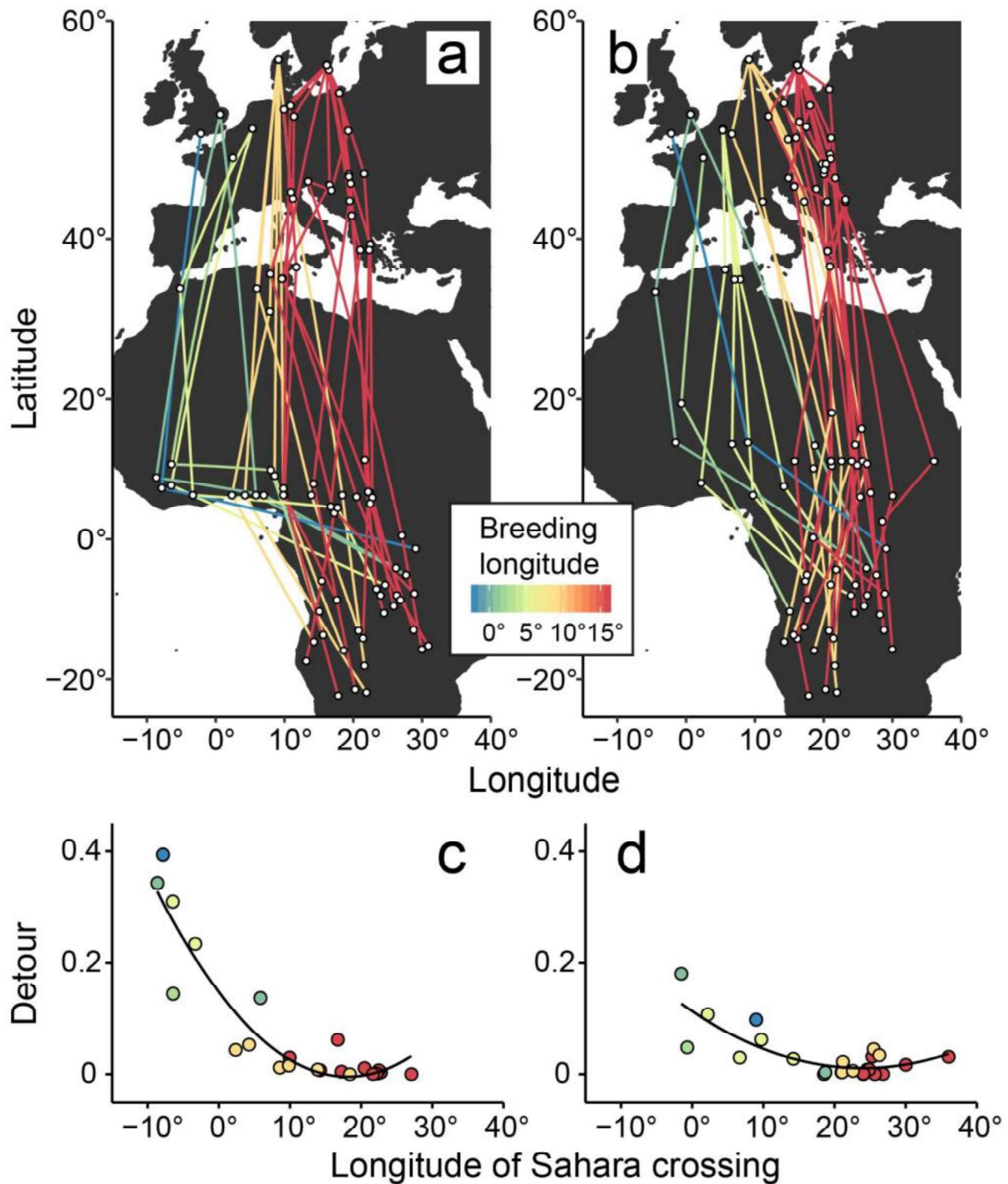
Aiming to further the study on the seasonal habitat matching of non-breeding visitors in sub-Saharan Africa we also investigated the temporal relationship between the movements of pallid swifts and local seasonality (**Paper IV**). Similar to the approaches used in studies on mammalian and avian herbivores (Bischof et al. 2012; Shariatnajibadi et al. 2014), we investigated the temporal inter-relationship between the seasonality in the local environment and timing of movements by the birds (**Paper IV**). This could prove to be a useful approach in a future analysis of repeated annual tracks of swifts as the degree of temporal coherency within individuals between years can be evaluated relative to yearly variations in environmental seasonality (Robillard et al. 2018). Given that the swifts are site faithful we would expect the birds to show plastic responses in departure timing relative to the local phenology as foraging conditions deteriorates (Terrill 1987).

## Spatiotemporal niche use in swifts

The temporal relationship between the withdrawal of the main rains and the arrival time of pallid swifts to the sub-Saharan non-breeding sites indicates that precipitation is an important factor shaping the non-breeding space-use of this species (**Paper IV**). We know from earlier studies that common swifts generally range further south in sub-Saharan Africa (Åkesson et al. 2012; Wellbrock et al. 2017). This indicates that common swifts may exhibit a shifted spatiotemporal movement pattern if they continuously track the same environmental niche throughout the non-breeding season. In our investigation on spatial and ecological segregation of the two swift species we found that common swifts upon arrival to sub-Saharan Africa used the northernmost sites (**Paper V**). Pallid swifts arriving weeks later settled further south. This spatial separation, however, resulted in very similar arrival timing in relation to the local end of the rainy season between the species, due to the southward movement of the main rains in the region (Nicholson 2012). As the two species undertook intra-tropical migrations the pallid swifts kept the temporal relationship relative to the withdrawing rains, while several common swifts undertook movements directly to their southernmost residence sites resulting in an average arrival about one month prior to the end of the rainy season (**Paper V**). It is tempting to associate the occurrence of the pallid swifts to this temporal shift in relation to habitat phenology in the common swifts, but the data is correlative and the information about actual competition between the species is still limited.

# The influence of external factors on migratory routes

It has become evident that birds commonly deviate from the shortest possible paths between the breeding and non-breeding areas resulting in detoured routes extending migration distances (Alerstam 2001; Lindström et al. 2011; Tøttrup et al. 2012). For example, in the common swifts documented detours added 53 % and 43 % to shortest distance in autumn and spring, respectively (Åkesson et al. 2012). While the detours in nightjars breeding in Sweden were more modest they resulted in a well-defined loop-pattern over northern Africa, where spring routes were consistently west of autumn routes (**Papers I, VII, VIII**; Figure 11). The observed loop-migration is not unique to European nightjars, and it has been documented by individual tracking in many species in several genera (e. g. Klaassen et al. 2010; Bradley, et al 2014; Willemoes et al. 2014). Regardless if birds strive to maximise safety, or minimise energy or time spent on migration (Alerstam and Lindström 1990), a uniform landscape with respect to foraging and flight conditions would probably result in birds mainly using the shortest (orthodromic) routes between sites. However, as topography and wind pattern vary over space the different strategies may lead to routes that deviates from the shortest one (Alerstam 2001; Erni et al. 2005; La Sorte et al. 2014; Kraunstauber et al. 2015). As actively flying birds generally spend the most time at stopovers (Alerstam and Lindström 1990; Hedenström and Alerstam 1997), route choice under the influence of habitat variation has been suggested as a potential determinant of flight paths alternative to the shortest one (Lindström et al. 2011; Hahn et al. 2014). While the result from a tracking study using several study sites within the Palaearctic-African migratory system was partially congruent with the expected route pattern, it did not provide a general explanation across flyways (Hahn et al. 2014). This suggests that we should look for other environmental variables that have the potential to at least partly determine the route shapes of Palaearctic-African migrants. In addition, in the case of the tracked nightjars, there was also a considerable longitudinal overlap between individuals between seasons, which is difficult to explain if preference for a certain habitat was the main driver of the observed loop-pattern (**Papers I, VII, VIII**, Figure 11).



**Figure 11 Detoured routes in European nightjars *Caprimulgus europaeus***

Maps illustrating the distributions of stationary locations as estimated from the tracking devices for spring (a) and autumn (b) respectively. Lines illustrate the direct (orthodromic) routes between locations and colour corresponds to breeding site longitude. The detour, measured as the extended fraction of the track in relation to the shortest routes between breeding and wintering sites for each bird for spring (c) and autumn (d) respectively. The fitted lines show the relationship between the longitude component of the location just south of Sahara and the extent of detour expressed as:  $y = 0.08 - 0.48x + 0.23x^2$ ,  $\text{Adj. } R^2 = 0.86$ , and,  $y = 0.03 - 0.15x + 0.09x^2$ ,  $\text{Adj. } R^2 = 0.632$  for spring and autumn respectively. From **Paper VII**.

As an alternative to the hypothesis regarding potential influence by the habitat *en route*, the effect of prevailing winds generated by stable atmospheric patterns of circulation is a promising candidate to explain loop-migrations (Erni et al. 2005; Kraunstauber et al. 2015; Shamoun-Baranes et al. 2017). Winds, operating at speeds of the same order of magnitude as the speed of the birds, can have a large influence on the progress of a migrant in relation to ground (Liechti and Bruderer 1998). It is therefore likely that birds have evolved properties to accurately evaluate and accordingly respond to winds (Liechti 2006). In fact, departures are generally undertaken in association with profitable winds, and in particular when wind changes to the better (Richardsson 1990; Åkesson and Hedenström 2000).

## Flight altitudes in relation to winds

While airborne, the birds should select altitudes where the combination of factors, such as wind, ambient temperature and humidity, air pressure, and oxygen partial pressure are most beneficial for migratory flight (Gautheraux et al. 2005; Liechti 2006; Liechti and McGuire 2017; Shamoun-Baranes et al. 2017). For the tracked nightjars we found a significant association between altitudes of the best wind profit and ambient temperature and the recorded altitudes of the birds (**Paper VI**). This is in general agreement with radar-based observations within the Palaearctic-African migration system describing bird aggregations in air-layers where winds are broadly aligned with the general migratory direction (Bruderer et al. 2018). Other factors such as ambient temperature and humidity, which is predicted to be relevant for the birds' water budget (Carmi et al. 1992) are less clearly associated with the altitude distribution of migrants (Schmaljohann et al. 2009). A possible explanation for this may be that birds select for profitable wind while flying and by timing the flight in accordance to the water budget, and by doing so, trade-off these competing selective pressures (Schmaljohann et al. 2009). This trade-off provides an additional potential explanation to why the tracked nightjars rarely undertook diurnal movements. Considering that a continuous flight would result in a reduced number of days spent on the Sahara crossing and the potential to lower risk and energy expenditure associated with the barrier crossing (Strandberg et al. 2009; Klaassen et al. 2014) the daily travel timing appear to be important in nightjars and other migrants when crossing the Sahara (Biebach et al. 2000; Schmaljohann et al. 2009; Bäckman et al. 2017; **Paper VIII**).

Similar to what has been found in radar-based studies (Bruderer et al. 2018), the altitudinal distribution of nightjars varied between regions, with high-altitude flights more common both over the Sahara desert and within sub-Saharan Africa (**Paper V**). This could be due to a higher propensity of the birds to fly low over more benign areas where the probability of encountering food concentrations is

higher. Alternatively it may be an effect of the general characteristics in atmospheric circulation patterns between the trade-wind zone and the temperate zone where local wind pattern and its variation is mainly driven by the passages of low- and high-pressure systems (Liechti 2006). Large-scale studies on altitudinal selection of individual migrants are still hampered by the low resolution in both environmental and tracking data and could likely benefit from local short-term investigation were other methods are available (e. g. Malmqvist et al. 2018).

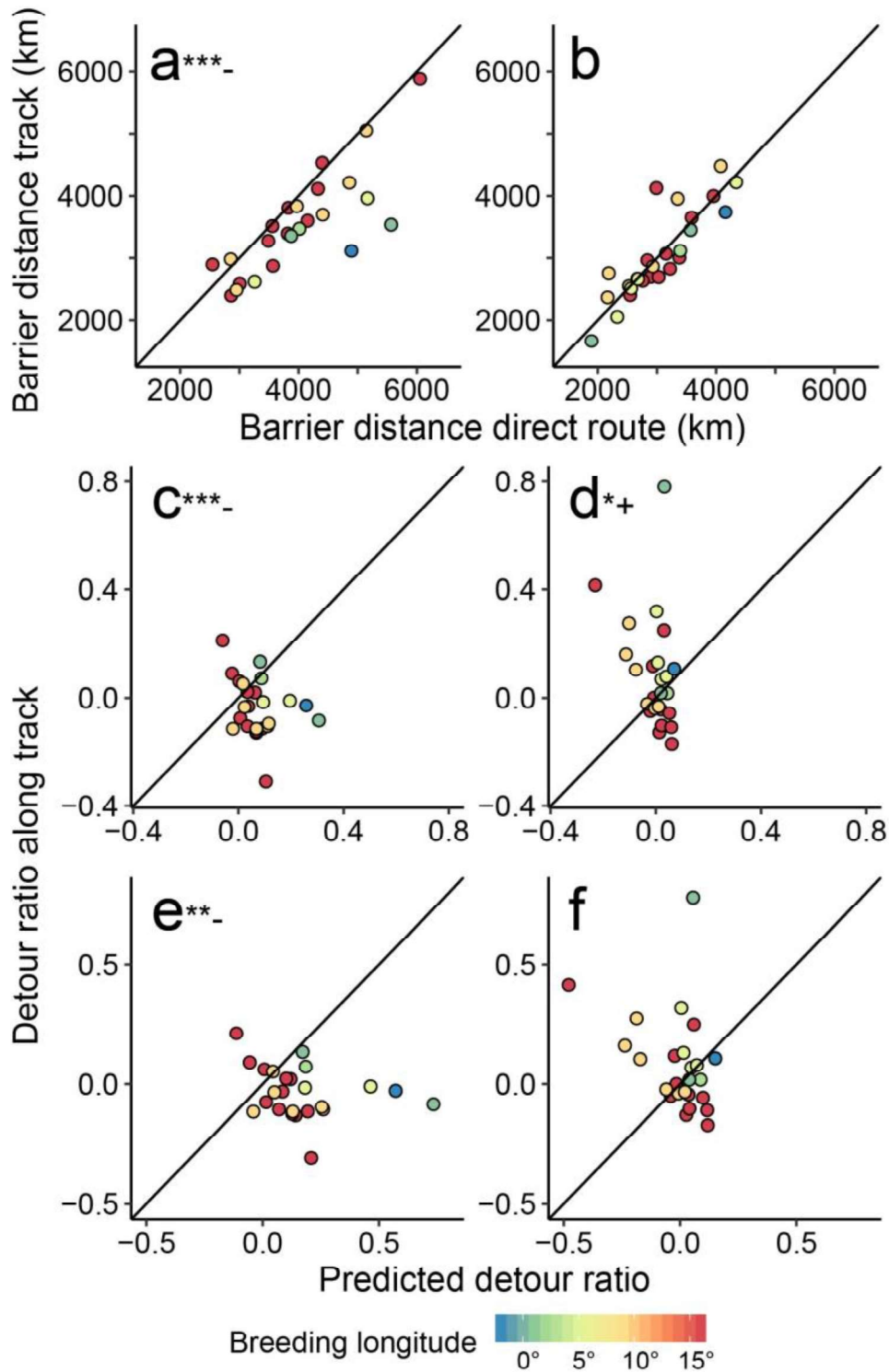
Based on GPS data from European nightjars presumed to be in migratory flights, we explored the association between the altitudinal variation of environmental variables, and their derivatives, and the sampled altitudes of the birds (**Paper VI**). One of the findings was that beneficial altitudes based on an estimation of wind profit including the added cost of side-winds consistently showed better associations with the birds' altitudes compare to altitudes based on the tail-wind component only. This suggests that one may consider using a wind-profit including the side-wind component, instead of the tail-wind component only, when analysing route choices in tracked migratory birds. Based on these results we used the side-wind influenced wind-profit estimates in our analysis of route selections in migratory European nightjars in **Paper VII**.

## Optimal routes and seasonal migratory connectivity

As tracks of nightjars from different sites in the European breeding range were documented (Evens et al. 2017; Jacobsen et al. 2017; **Paper I**; Figure 11), it became evident that the movement pattern of the species varied in relation to breeding longitudes. In **Paper VII** we investigated to what degree the migratory connectivity between breeding and non-breeding sites varied across the non-breeding season (Salomonsen 1955; Webster et al. 2002), and if the movement pattern was associated with the interaction between wind, topography and migratory strategy (Alerstam 2001; Liechti 2006).

We demonstrated that according to the energetic principles of Alerstam (2001) the detoured routes documented in the nightjars indeed could be preferable for energy-minimising migrants after accounting for prevailing wind conditions (**Paper VII**; Figure 12). In contrast to the hypothesis that the stopover habitat en route is a main determinant of the routes of Palearctic-African migrants (Hahn et al. 2014) we show that the prevailing wind pattern over the Saharan desert can shape the routes of energy-minimising migrants similarly to what is observed in large parts of the migration system (**Paper VII**). An ultimate test for the wind-hypothesis would be to accurately predict if and where a breeding longitude of European nightjars would result in a counter-clockwise loop-migration pattern superior to the clockwise loop-migrations observed among the tracked nightjars.



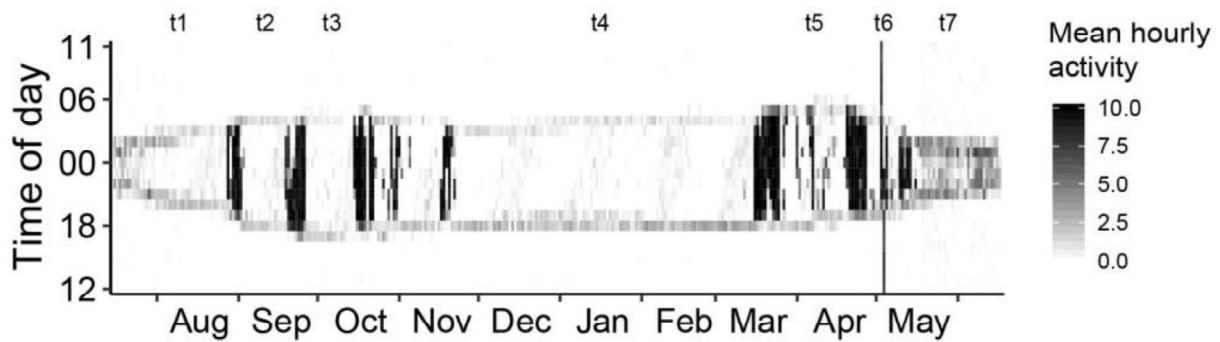


**Figure 12 Comparisons between detoured, and direct routes in European nightjars *Caprimulgus europaeus***  
 Linear relationships in spring (a, c, e) and autumn (b, d, f) for barrier distance along the direct route and track (a and b); and calculated values corresponding to the direct (orthodromic) route and the track according to eq. 2 (c and d) or eq. 1 (e and f). The lines represent  $x = y$  and dots falling below the lines corresponds to occasions when tracks resulted in a shorter barrier crossing, (a and b), or lower calculated transport costs (c-f) than the direct route. Significant differences are denoted with a "\*\*\*" and a "+" or "-" if the tracks resulted in a higher or lower values, respectively. Colours correspond to the breeding site longitude. From **Paper VII**.

In red-backed shrikes *Lanius collurio* breeding in Sweden the loop-migration pattern was demonstrated to be counter-clockwise, with spring routes to the east of autumn routes (Tøttrup et al. 2012) This was counter to the predictions based on European nightjars in **Paper VII**, indicating that other factors such as habitat quality en route, historical range expansions and navigational constraints, or a combination of them also may influence the patterns of migration routes (e.g. Hahn et al. 2014; Sokolovskis et al. 2018). In the case of European nightjars, the currently available data from archival GPS' should allow for a more robust assessment of the relative importance of flight conditions and habitat quality for determining the shape of migration routes.

# Temporal constraints on migrating nightjars

Let us return to the possible constraints acting upon the fuelling rates and migration speeds in flapping-flying migrants. Although fuelling capacity may approach 10 % of the lean body mass of the individual if allowed to fuel around the clock (Kvist and Lindström 2000), daily fuelling rates in the wild are generally more modest (Lindström 1991). The importance to maximise fuel deposition rate has been put forward as one of the explanations why birds generally migrate during the night when fuelling is not possible anyway, as it allows birds to resume fuelling after a flight without any unnecessary waiting time (Alerstam 2009). As an apparent paradox, one of the species undertaking the longest annual migrations within Palaearctic-African migration system is the European nightjar. As it is assumed to be strictly crepuscular and nocturnal also outside the breeding season, available daily foraging time therefor overlaps with periods of migratory flights. In **Paper VIII** we demonstrated that nightjars, as expected, only exceptionally show continuous diurnal activities, which were associated with the crossing of the Sahara desert and the Mediterranean Sea (Figure 13). The daily travel speeds varied between regions, something we associated with the differences in habitat that the birds were passing. Over the Sahara desert where the food availability is relatively low, the birds likely allocate more time on a daily basis towards flight, while the more benign areas in Europe may motivate them to interrupt flights and spend more time foraging (Klaassen et al. 2008). This pattern was however less clear when analysing movements within sub-Saharan Africa, but that may have been due to the relatively coarse division of regions. As a result this region may include both a less hospitable tropical rain forest (Strandberg et al. 2009) and a part where migrants pass the non-breeding areas of the species where foraging conditions presumably are relatively profitable.

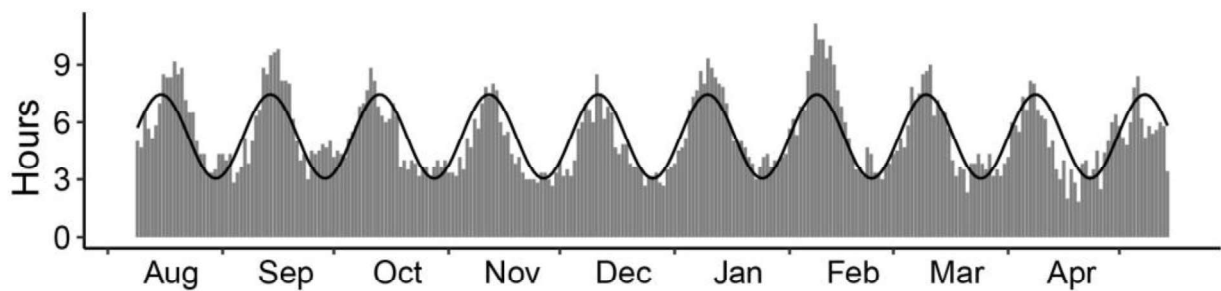


**Figure 13 The annual activity pattern of an European nightjar *Caprimulgus europaeus***

When plotting the hourly activity pattern across the annual cycle a few clear patterns emerge. First, the activity in the two breeding seasons (t0 and t7) is confined to a few hours in the middle of the night, whereas the daylight hours mainly lack any activity registrations. In autumn, as the nights become longer (or when the bird fly southward), a symmetrical increase in the daily spread of activity can be observed. Migratory flight segments, when the bird continuously flaps its wings for several hours, elevate activity registrations here illustrated with dark lines throughout the nights. Patches of dark lines highlight flight episodes where flight segments from consecutive nights were aggregated. In spring, presumably associated with the crossing of the Mediterranean Sea, a single nocturnal flight extends across the day and ends in the middle of the following night (t6). The nocturnal activity pattern in the non-breeding season outside the flight episodes show few activity registrations and relatively larger amounts of registrations are found in association with dusk and dawn (t2-t5). The diagonal shaded bands seen throughout the annual cycle were associated with the moon cycle. From **Paper VIII**.

Peculiarly, we could also confirm a periodic relationship between daily activity and lunar phase throughout the non-breeding season (**Paper VIII**; Figure 14). This activity pattern has earlier been described in two species of tropical nightjars where it was shown to be positively correlated with insect abundance (Jetz et al. 2003), and there are also suggestions that European nightjars at least to some extent synchronise breeding events with the lunar cycle (Perrins and Crick 1996). It has become increasingly apparent that the association between the lunar cycle and animal behaviour is a widespread phenomenon either directly by influencing melatonin production in the animals or indirectly by affecting e.g. foraging efficiency (Kronfeld-Schor et al. 2013; Numata and Helm 2014; Yamamoto and Trathan 2015).

The lunar cycle has been linked to foraging behaviour in nocturnal species of several groups that depend on vision for detecting and catching prey, such as seabirds (Pinet et al. 2011; Cruz et al. 2013; Dias et al. 2016), nightjars (Jetz et al. 2003), but also in shorebirds foraging in intertidal zones (Zwarts et al. 1990; Calle et al. 2016). Given that foraging behaviour is linked to fuelling rates, it is likely that the temporal setting in the annual cycle of some migratory birds will be influenced by the periodicity of the lunar cycle. For the nightjars studied in **Paper VIII** we could describe a temporal relationship between the full moon and the fraction of birds performing a migratory flight. The observed time lag of about a week indicates that the general migration intensity increased after a period of presumed elevated foraging conditions (**Paper VIII**). A periodic temporal variation in daily fuelling rates is particularly intriguing because it puts further dynamics into the ways migrants can or will behave optimally. The influence of dynamic foraging conditions on the adaptive values in migrating birds is yet to receive full attention and may push for an extension of the optimization models used in migration research of today.



**Figure 14 Lunar-associated periodicity in non-breeding European nightjars**

The average daily number of hours with registrations of presumed foraging activity of the 5 birds with data covering the 2016-2017 non-breeding season. Superimposed is a sinuous curve with a 29.53 day periodicity approximating the moon cycle within the non-breeding range throughout the non-breeding season. The curve was fitted through an iterative process in which the starting date varied until the highest  $r^2$  value was reached. The starting date (2016-08-10) of the curve corresponds to a moon in its first quarter. The fitted values varied between 3.0 and 7.4 hours indicating that potential daily foraging time increases with about 150 % in full moon nights relative to nights with new moon. From **Paper VIII**.



# Conclusions and future perspectives

In this thesis I have investigated aspects regarding the movement ecology of aerial insectivorous birds by studying the non-breeding activity in three long-distance migratory species within the *Apus* and *Caprimulgus* genera. Although I have restricted my studies to birds that catch aerial prey while on flight, the questions, observations and conclusions presented here should be applicable also to many other flapping flying avian migrants. The use of different types of miniaturised devices designed to record position, activity pattern, or environmental variables such as ambient light and air pressure, allowed me to study the movements across seasons on an individual level, and revisit questions that earlier have been approached on a population level. Studying animal movements on both an individual and population-level will most likely continue to complement each other with potential synergetic effects when combined (e. g. Nilsson and Sjöberg 2016).

We found empirical evidence that the two swift species are predominately aerial throughout the non-breeding season and that regular landing events are restricted to their (short) visit to the breeding site (**Papers II, III**). Despite their mobility and predisposition to truly track resource waves across their African non-breeding ranges, they exhibit a movement pattern similar to terrestrial species where longer periods of residence alternate with short durations of directed movements (**Papers IV, V**). Combined with documented interannual site faith-fidelity, the observations suggest that factors such as patchiness of resources and prior local experience are advantageous also in mobile and apparently free-ranging species.

Linking phenological events to the timing of animal movements enables comparison between populations and species about how they time their movements relative to the environment, an emerging question in movement ecology in the face of climate change (Both et al 2006). In combination with investigations on migratory connectivity, the relative habitat match, (and other correlates) between animal and environment may prove useful to link directional habitat change to breeding population trends (**Paper IV**). In **Paper V**, we used the temporal relationship between the rainy season and site arrival to investigate the non-breeding niche-use of common and pallid swifts in West Africa. For small and wide-ranging migratory species, finding platform-derived environmental factors as candidate proxies for drivers modulating the birds' spatiotemporal distribution may often be the cheapest, if not the only, way to further understand the large-

scale ecology of their movements (Pettorelli et al. 2005). However, linking prey availability to platform-derived environmental proxies is challenging, in particular in the study of predators associated with mobile and ephemeral food sources such as flying insects, which are often too elusive to measure. A new promising approach in studying the interaction between aerial insectivores and their prey is the use of a Lidar system developed for studying simultaneous flight activity of groups of small (e. g. insects) to medium-sized organisms such as birds and bats (Malmquist et al. 2018). This method should also allow sampling of aerial prey distribution which could be linked to environmental proxies.

Individual-based tracking has revealed that detoured routes and loop-patterns are universal in long-distance migrations. Similar to the effect of currents and streams on the trajectories of aquatic animals (Hussey et al. 2015), the structure of the air-space, with wind as the major player, is important in shaping the routes of aerial organisms (Liechti and McGuire 2017; Shamoun-Baranes et al. 2017). In our investigation of the loop-migrating nightjars the documented pattern during spring migration conformed well to the predicted routes derived from the interaction of prevailing winds and energetic principles of long-distance flights (Alerstam 2001; **Paper VII**). This result along with the observations that the pre-barrier stopover sites were rather evenly distributed across longitudes, and that the sites of the Swedish birds overlapped between seasons suggest that winds en route are more important in shaping migration routes than stopover habitat – at least in the case of European nightjars (**Papers I, VII, VIII**). Studies in the near future will likely elucidate more details of the wind-related strategies used by European nightjars and other small avian migrants across flights and seasons.

The proposed occurrence of a dynamic foraging opportunity (and hence daily fuelling rates) in the European nightjar (**Paper VIII**) is a new and exciting concept in the field of optimal migration that hopefully inspires further theoretical and empirical explorations. What rules should for example a time-minimising migrant adopt in a landscape where fuelling varies over time and not space, and under what conditions will we find effects of lunar periodicity on migrants' behaviour? Adding to the apparent correlation between the daily number of moonlit hours and potential fuelling capacity highlighted in the European nightjars, there are likely many other species whose migration strategies could be similarly influenced by the periodicity of the lunar cycle. Wading birds dependent on tidal mudflats (Zwarts et al 1990; Calle et al. 2016) and shallow-diving seabirds utilising lunar-phobic marine prey (Gilly et al. 2006; Cruz et al. 2013; Dias et al. 2016) are two large avian groups where several species undertake some of the most stunning large-scale annual movements (Gill et al. 2009; Pinet et al. 2011). How dynamic fuelling may influence the spatiotemporal progression in animal migration and to what extent it affects the migrants' temporal variation are exciting questions for further studies.



A challenging, but nevertheless relevant, aspect is the linkage between the non-breeding and breeding seasons (and vice versa) through various carry-over effects (Marra et al. 1998; Norris 2004). With GPS-tags and other techniques becoming efficient enough to record space-use and migration routes with high spatiotemporal resolution, correlative studies on how events in different parts of the annual cycle carry-over into subsequent events and ultimately affects reproductive success and the fate of the individual will be possible (Both et al. 2006; Ouweland and Both 2017). The European nightjars could prove to be a useful system to study questions regarding carry-over effects as they are large enough to carry devices enabling year-round tracking, and may be a natural experimental design as their migration relates to the continuously alternating calendar timing of the lunar cycle (**Paper VIII**). However, their crepuscular and nocturnal habits also add some interesting challenges when studying their breeding ecology, which is a necessity to document fitness.

The study of animal movement is currently mainly driven by the miniaturisation of technical devices and often by the desire to explore and describe the whereabouts of continuously smaller and smaller species (McKinnon and Love 2018). But as such studies are combined with theory-driven and experimental investigations the future of movement ecology research looks bright and exciting.

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**Field work**

Aron Hejdström has taken several brilliant photos of my work and for that I am thankful. This is one illustrating me handling one of many nightjars trapped during the project.